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Review Article

Water Level Fluctuation Effect on Fish Reproduction Success

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Alteration of water levels of the lake/reservoir due to changes in river discharges, upstream abstraction, and drawdown regulation due to hydropower generation has been reported as among the major challenges to fish physiology and ultimately reproduction. Variations in lake/reservoir water levels influence biodiversity and the abundance of lake/reservoir biota. Variations have the greatest impacts in the littoral zones hence, interfering with fish spawning, incubation, and hatching of eggs, as well as the development of larvae, postlarvae, and juveniles. This particular paper reviews the literature available on the effect of the reservoirs/lakes' water level fluctuations on fish reproduction success using the documentary view method. The literature argues that water level fluctuations have both positive and negative impacts depending on frequency, magnitude, and duration and the species exposed. Extreme fluctuations tend to bring more adverse impacts. It further indicates that extreme and untimely water level fluctuation has direct impacts on the aquatic habitats and ultimately impacts fish assemblage and their populations. Few articles indicate the range of decrease or increase of water level, duration of such events, and effects they have on reservoir/lake ecosystem functions and fish physiology. Nevertheless, quantification of moderate and extreme water level fluctuation and associated effects is lacking. Although water level fluctuation is an important environmental cue for aquatic organisms, literature shows that the reduction of extreme water level variations especially multiannual variations is vital for fish reproduction. Therefore, upstream water use and reservoir operations should take into consideration the effects of water level fluctuations on reservoir structure, biological functions, and ultimate effects on fish reproduction.

1. Introduction

Global freshwater demand is increasing dramatically, with water withdrawal rates more than tripling in the last five decades. Alteration of water levels of the lake/reservoir due to upstream abstraction, drawdown for hydropower generation, and climate changes have been reported among the major challenges inhibiting fish yield. Human-induced amplification of water level fluctuations has become one of the major global disturbances of aquatic ecosystems, endangering the integrity of both aquatic and associated terrestrial ecosystems [1].

Due to the economic motivation for the construction of reservoirs, their hydrology is usually highly determined by its management, which is oriented to provide more services to humans such as hydropower generation, irrigation, and urban water supply. Overexploitation of water resources from the reservoir or its rivers has been pointed to increase seasonal and interseasonal fluctuation amplitudes [2]. Maintenance of reservoir conditions to support biological communities including fishes often receives less thought. The problem is likely to be exacerbated by predicted increases in climatic variability and enhanced demand for water and hydropower, which may considerably affect global aquatic biodiversity including fish mainly because of the potential to disrupt their physiological functions including reproduction activities [1].

Water level fluctuation is recognized as one of the dominant forces controlling the function of lakes/reservoir ecosystems [3]. Literature has widely demonstrated the effects of water level fluctuation, emphasizing that reservoirs or manmade lake ecosystems are the most affected [2, 4].

Shallow lakes/reservoirs are reported to experience considerably larger ecological impacts of water level fluctuations than deep lakes [2, 5, 6], whereas, in deep lakes/reservoirs, the littoral region is often the only affected region [1, 4].

Water level fluctuations occur naturally or as human-induced water level variations. Their effects on the biota can be beneficial or adverse [7–9] depending on local conditions where they occur [4]. Both positive and negative effects of reservoir/lake water level fluctuations are widely discussed. Natural, gradual, and predictable water level fluctuations are essential for the survival of diverse aquatic species, and support the biological and reproduction activities of fish in the reservoirs/lakes. On the other hand, altered water level variations interfere with the integrity of the whole reservoir/lake systems [1, 2, 8, 10].

Periodic high water levels or floods have been linked to positive benefits to aquatic systems due to their potential for replenishing nutrients and other materials for the development of plant communities and local ecosystem processes [3, 11]. Persistent high water levels are also linked to littoral zone vegetation type shift with a cascade effect on fish reproduction [3]. On the other hand, extreme drawdowns are often associated with the most adverse impacts on aquatic ecosystems. Thus, water level fluctuations can reduce the reproduction success and biological diversity of the reservoir/lake. One of the ways in which water level fluctuation causes this is through the loss of productive habitats. Habitats that support high levels of primary productivity, such as shallow wetlands and littoral zones, are particularly sensitive to water level fluctuations. Rapid changes in water levels can disrupt the growth of aquatic vegetation and algae, which form the base of the food web and provide essential energy and nutrients to higher trophic levels. Reduced primary productivity can lead to a decline in the abundance and diversity of organisms throughout the food chain. In addition, fluctuations in water levels can favor certain species over others, leading to shifts in species composition within aquatic communities. Species adapted to tolerate or exploit the conditions created by fluctuations may thrive, while others less able to cope may decline or disappear. This can result in reduced diversity as some species are lost from the ecosystem.

The littoral zone is the most likely habitat to be affected by reservoir drawdown including some fundamental processes such as organic matter decomposition rate, feeding patterns, and trophic interactions among organisms and energy flow [12]. This is because they quickly experience changes such as submersed or exposure [13]. The frequency and extent of drawdown leading to shoreline exposure have also been associated with the presence or absence of a littoral zone community, the structure of sediment, and the supply of nutrients and organic materials [13]. Findings by Furey et al. [12] reported that Sooke reservoirs which experienced frequent drawdowns of up to 6M had a lower density of microphytes than lakes which experienced a drawdown of 1 m maximum.

Reservoirs/lakes are traditionally characterised by static morphological or chemical parameters such as depth and dissolved solids, while the dynamic impact of shifting water supplies has received little attention [1]. Water level fluctuations also have the potential to change the physiochemical environment of the reservoir by modifying habitat structure at the shallow water and inflow zones, the sediment-water interface, or internal nutrient loading regimes [1, 14–17]. Drawdown affects the thermal structure, light environment, and sediment exposure, whereas these changes affect biological, chemical, and physical processes, especially in the littoral zone.

Kotut et al. [13] reported that river inflows exert the greatest influence on the limnological conditions of the reservoir. Flood inflows lead to a decline in the Secchi depth, electrical conductivity, and total alkalinity. Peak levels of these parameters characterize periods with no inflows. On average, high nutrient levels and loading occur during periods of increased river inflow. In addition, Yin and Yang [3] observed low ecological degradation and the highest species richness corresponding to the high water level in one of the 16 cycles that occurred between 1951 and 1966 in Baiyangdian Lake (China)

Fish species evolved to adapt to a range of water depths and water level variations [8, 14, 18, 19]. They naturally respond directly to the effects of wave disturbances and indirectly to the modification of substrates. In addition, water level drawdown has the potential of eliminating fish species, which are unable to retreat to the open water. They can be replaced with species that are well-adapted to fluctuations [20]. Weiperth et al. [6] associated low water levels due to global climate change with a decline in the fish stock of Lake Balaton. Weiperth et al. [6] found that largemouth bass and crappie recruitment were positively related to the water level. Strong-year classes were observed in years with high water levels. In addition, the reproduction success of pikeperch due to the decrease in the population of its predator, the largemouth bass following low water levels was observed [6].

Water level fluctuations can have a significant impact on fish physiology. When water levels fluctuate rapidly or frequently, it can cause stress to fish, affecting their behavior, growth, and reproduction. Changes in water levels can also cause a shift in water temperature, dissolved oxygen levels, and nutrient availability, both of which are critical factors affecting fish reproduction. For example, rapid increases in water levels can lead to temperature fluctuations and decreased oxygen levels, which may impair embryo development and reduce survival rates. Conversely, stable water levels can help maintain suitable temperature and oxygen conditions for reproductive success. Furthermore, if water levels drop rapidly, it can cause fish to become stranded or trapped in isolated pools, which can lead to mortality. On the other hand, if water levels rise too quickly, it can cause fish to be swept downstream or disorientated, leading to injury or death. In addition, changes in water temperature due to fluctuating water levels can affect fish metabolism, respiratory rates, and immune function. This can lead to increased stress and susceptibility to disease. This study therefore wishes to explore the available knowledge on the effect of water level fluctuations on fish reproduction success.

1.1. Contextual Framework of the Study. This particular review explores the literature available to analyze the effect of the reservoir water level fluctuation on fish reproduction success (Table 1). The paper focuses on the effects of water level fluctuation on fish habitats, feeding, and reproduction success. The review uses a systematic approach to gather articles for the review, and a qualitative method, to review pieces of evidence supporting the effect of water fluctuation on fish reproduction success. The review is motivated by the effects of climate changes on the potential of reservoir fisheries as manmade freshwater bodies under the growing demand for protein due to human population growth. Fishes having huge potential to provide affordable protein are physiologically challenged by the impacts of climate change and human activities on freshwater bodies including reservoirs. The drop has been linked to the ecological dynamics of the reservoirs/lakes' hydrology dynamics. The review involves papers on water level fluctuation effects on fish reproduction success in reservoirs and natural lakes, published worldwide (Table 1). The review was limited to recently published papers between 2000 and 2023, but a few papers from the 1970s were included because of their relevance in terms of the content (Table 1). The compilation of this review is an important analysis of the available knowledge on the topic considering growing anthropogenic and climate change influences on aquatic ecosystems.

1.2. Data Analysis. This study used a qualitative method systematic review for analyzing the effect of water level fluctuation on fish reproduction success. A qualitative analysis was performed, with a total of 50 articles, theses, and dissertations (Figure 1). In this procedure, the articles were qualitatively analyzed on the effect of water level fluctuations on fish reproduction success. The analysis involved the effect on fish habitat considering its importance of food availability, shelter, and protection of eggs and juvenile fish. Other issues of water level fluctuations relating to fish reproduction successes, such as fish physiology, energy usage, and food web and feeding relations were investigated. The quantitative analysis was extracted specifically from articles, book chapters, and reports.

2. Results

There exist several collections of literature that build into the topic of water level fluctuation effects on fish (Table 2). Some articles address water level fluctuation effects on fish habitats in general; some are specific to the effect on littoral zones, or shallow water, water quality, and aquatic vegetation (Table 2). Others link the water level fluctuation to fish energy usage, food webs, fish physiology, and fish breeding success (Table 2). Through analyzing these research themes, this review explains the impact of water level fluctuations on fish reproduction success. Subsequently, this section presents the results of the qualitative analysis performed in this review.

2.1. Water Level Fluctuation Effects on Reservoirs/Lake Fish Habitats

2.1.1. Habitat Heterogeneity. One of the most prominent effects of water level fluctuation is the loss of aquatic habitat heterogeneity vital for fish reproduction [7, 9, 20, 40]. The extreme water level fluctuation influences the abundance of the coarse substrate, submerged vegetation, and shade. High water level leads to the formation of complex habitats, whereas significantly lower water level reduces habitat heterogeneity, especially in the littoral zones. In their experiment, Logez et al. [5] observed an increase of habitat complexes available for fish during the highest water levels. Their results also showed a pronounced relationship between habitat complexity and fish assemblage which changed along with the water level gradient. Logez et al. [5] reported further that there was an increase of sites with a thin substrate and low slope following the water level decrease. Areas with fine substrates provide a low structural complexity and fewer refugees, while a coarse substrate provides intermediate habitat complexity.

Habitat homogenization during low water levels was also reported by Gasith and Gafny [4] and Zohary et al. [2] in Lake Kinneret. The percentage of shorelines covered by small particles increased from 6% to 49% with a 3 m decrease in water level. They observed an increase in a thin substrate, while coarse substrates decreased resulting in loss of littoral zone habitat complexity. Course substrates are the preferred habitats for breeding and juvenile fishes. In a mesocosm experiment carried out by Fischer and Öhl [22], 70.4% of fish tested solitarily selected the largest shelter tube. When they were put in a group of nine fishes, fishes competed for large tubes/shelter, and the largest fishes were successful in defending their preferences compared to smaller conspecifics. Furthermore, they discovered that adequate daytime shelter availability in sufficient quantity and quality was an important resource, for juvenile fish's behavior and growth.

2.1.2. Colonization of Aquatic Vegetation. Water level fluctuation enhances or restricts the colonization of vegetation. Evtimova and Donohue [1] linked amplified water level fluctuation with reduced macrophyte diversity and vegetation cover of the littoral zone. In their survey, the authors in [25] reported that transects that were flooded and then dewatered supported 43 taxa, whereas transects that were flooded for at least six years contained 11 taxa. The disappearance of submerged vegetation and riparian shade due to an increase in water level fluctuation has been reported in the Bariousses reservoir, in West-Central France [1].

The amplitude of water level fluctuations may strongly determine the development of macrophytes in lakes/reservoirs [27, 29]. Drawdown, for instance, is a prerequisite for the successful germination and survival of various macrophyte species. It significantly affects macrophyte composition. In addition, disturbances caused by drawdown may prevent competitive dominance, thereby increasing species richness [27]. Consequently, species richness of macrophytes is enhanced by increasing the amplitude of water level fluctuations [27]. Nevertheless, large water level fluctuations may eliminate species that are sensitive to prolonged submersion, such as certain helophyte species.

Vegetated habitats are known to have a greater diversity of life forms due to their higher complexity [5]. Scharf [28] found that inundated vegetation during high water provided quality-spawning habitat for adults and provided food and

Table 1: Inclusion and exclusion criteria for articles in the review.

Criteria	Included	Excluded	Justification for criteria application
Publication date	2000 to 2023	Before 2000	Used collections from trusted databases to analyze the effect of water level fluctuation on fish reproduction success
Language of publication	Articles published in English language only	Articles not written in English	Due to authors' knowledge of English language only
Theme of publication	Articles on water level fluctuation effect on fish reproduction	Articles outside the scope of the effect of water level fluctuation on fish reproduction	To get articles on the scope of the effect of water level fluctuation on fish reproduction
Availability of the article	Fully available open-access articles	Complete articles not available	Article/publication requiring purchasing were unavailable to the author
Type of article	Peer-reviewed research journal articles	Conference abstracts, unavailable book chapters, review papers, and bibliometric and meta-analyses	Interested in available peer-reviewed empirical or original research
Country or location of the study	Study area	None	Articles from various countries and regions where studies on the effect of water level fluctuation on fish reproduction success were included

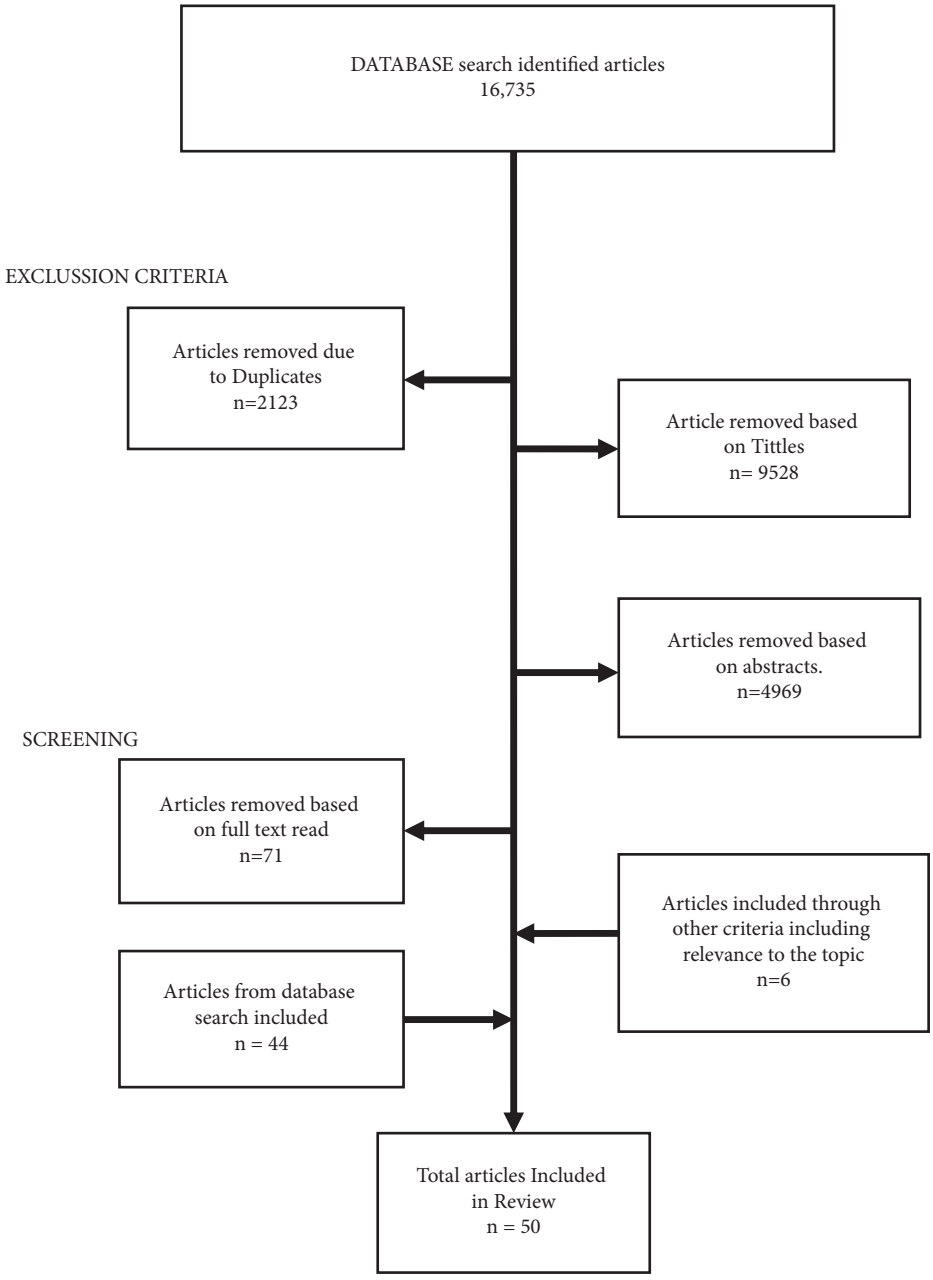

Figure 1: Protocol followed for article selection.

shelter from predation for largemouth bass yearlings, which thus, enhanced their recruitment as compared to years with low water levels. In support of this argument, Brauns [21] found that the community composition of rooted habitats significantly differed from that of coarse woody debris and sand. Abundances of Coleoptera and Trichoptera and abundances of the piercer, predator, shredder, and xylophages species were significantly lower in the sand than in rooted habitats [26].

Water level fluctuation has been also reported to affect the coverage of aquatic plants. A recent study by Wen et al. [29] reported a variation of coverage that they called the lower distribution boundary of the three species of macrophyte in Erhai River, China. In their three-year study, they found that the responses of the three submerged microphyte species to water level fluctuations were divided into three periods: recovery growth period, stress tolerance period, and recession period. The three species showed similar variation patterns. During the recovery growth period, when the water level decreased by 0.3 m, the lower distribution boundary of *V. natans*, *C. demersum*, and *P. maackianus* decreased by 0.31 m, 0.64, and 0.50, respectively. During the stress tolerance period, the water level increased by 0.7 m and the LDBs of *V. natans, C. demersum*, and *P. maackianus* increased by 0.04, 0.13 m, and 0.35 m, respectively. During the recession period, when the water level decreased by 0.5 m, the lower distribution boundary of *V. natans, C. demersum*, and *P. maackianus* increased by 0.2 m, 0.11 m, and 0.22 m.

Table 2: Classification of reviewed articles.

S/N	Themes	Frequency of the topic	Citations
1	Fish habitat and littoral zone habitats	15	[1, 4, 5, 7, 8, 10, 11, 19, 21–25]
2	Aquatic vegetation, microphytes, and macrophyte	13	[9, 16, 19, 21, 25–29]
3	Water quality (turbidity and internal nutrient loading/cyanobacterial blooms)	10	[1, 4, 12–17, 20, 30]
4	Predation	5	[2, 22, 31, 32]
5	Food web and invertebrates/	3	[8, 20, 33]
6	Fish physiology	4	[5, 6, 19, 34]
7	Energy use		[24, 35–37]
8	Fish breeding success	20	[1, 6, 7, 11, 14, 15, 31, 34, 38–46]

Aquatic vegetation plays a crucial role in supporting fish reproduction by providing habitat, shelter, food, and spawning grounds. Many fish species rely on aquatic vegetation as spawning habitat. Submerged plants, such as water lilies, pondweed, and eelgrass, provide suitable surfaces for fish to deposit their eggs. These plants offer protection from predators and help to prevent eggs from being swept away by currents. Vegetated habitats also serve as important nursery areas for juvenile fish. Dense stands of plants offer shelter and protection from predators, allowing young fish to grow and develop in relative safety. They also contribute to the food web by providing a habitat for algae, invertebrates, and other small organisms that serve as prey for fish. Fish may forage among the plants, feeding on insects, crustaceans, and detritus associated with the vegetation. In this way, aquatic vegetation indirectly supports fish reproduction by providing essential food resources throughout their life cycle. Changes in vegetation abundance or composition can alter the availability of food resources for fish, potentially affecting reproductive success.

2.1.3. Shallow Water Habitats (Littoral Zones). Littoral zones are the regions of shallow water extending from the shoreline of a lake to the maximum depth (1–5 m) at which light still reaches the bottom sediments to allow macrophyte growth [16]. Their location shifts with a change in water level leading to physical substrates alternating between being exposed and inundated [2, 4]. These zones create an interface between the terrestrial ecosystem and the pelagic zone, constituting habitats for both terrestrial and aquatic organisms [2]. The ecotone is the most productive part of an aquatic ecosystem because it combines both terrestrial and aquatic processes, which alternate under fluctuating water levels.

The littoral zone has a greater heterogeneity of the physical structure than the aquatic habitat of the pelagic zone [5, 38, 47, 48]. Hence, it shelters the majority of the biological diversity of reservoirs/lakes [1, 41]. Evtimova and Donohue [1] identified several specific ways through which water level fluctuation modifies littoral assemblages along the depth gradient. Their study identified separate pressures according to basing water levels, that they suggested to be used as indicators to be employed and demonstrates the need to mitigate the most extreme water withdrawals.

Water level fluctuations are the major functions of reservoirs that have the greatest effects in the littoral zones. Large areas of littoral regions are easily converted to air-exposed habitats even with a small water drawdown. Extreme and untimely water level fluctuations act as hydrological stressors to biological communities in the littoral zone of reservoir/lake. Zohary et al. [2] reported that fauna and flora of reservoirs/lakes with extreme water level fluctuations are strongly depressed and consist of a restricted number of ephemeral species, such as insect larvae. Baumgärtner et al. [49] reported high abundances of invertebrates correlated with the high water level. They added that the high abundance was due to the availability of settlement areas, supporting the hypothesis that space is a limited resource in the littoral zone, at least for some invertebrates. In another study, water level fluctuations threatened the existence of littoral zone submerged vegetation in East German lowland lakes [21].

Many fish species are critically dependent on shallow littoral areas for spawning, rearing, and feeding during their early development period, and therefore any fluctuation during this period could have detrimental effects on year-class recruitment [41]. Different fish species use the zone of fluctuation at differing times of the year. According to Kahl et al. [41], the littoral zone is an important spawning habitat for largemouth bass and roach. Juvenile roach uses this habitat as a place of refuge from predation. Weiperth et al. [6], who analyzed the effect of water level fluctuation on the anglers' catch, reported that the decrease in anglers' catch data was observed in many years, when the water level was drawn back from the littoral zone. They further discovered that eel and catfish had the highest abundance in the littoral, because they were able to find appropriate food and shelter in the reed and along the ripraps.

Many fish use the littoral zone at spawning and as juveniles but the pelagic as adults, and hence their life cycle and reproduction depend on littoral resources [16]. Such species provide a littoral-pelagic link and the loss of their littoral habitat may have cascading effects influencing the entire lake ecosystem [4]. Loss of reed beds at low water levels in Lake Biwa led to reduced survival of the larvae of the cyprinid fish *Cyprinus carpio* and *Carassius* spp [16].

2.2. Water Level Fluctuation Effect on the Food Chain and Feeding Relationship

2.2.1. Nutrient Loading and Recycling. One of the major roles of changing water levels is the injection and resuspension of nutrients [15]. Nutrient conditions of lakes and reservoirs associated with rivers are predominantly dependent on the inflowing material from the catchment [30]. According to Lima et al. [15], biogeochemical cycles are strongly influenced by periodic increases in water levels, because in addition to the direct exchange of nutrients resulting from these dynamics, floods promote nutrient pulses from the decomposition of flooded vegetation. In addition, constant up and down shoreline movement facilitates nutrient recycling by fluctuating redox potentials. This strongly suggests that nutrient supplies from both affluent rivers and the flooded marginal areas stimulate fish production in lakes and reservoirs [30]. Primary productivity and the biophysical responses of the aquatic vegetation, and of several taxa of invertebrates, are also dependent on the water level fluctuations [15].

Reservoirs that experience annual drawdown exceeding mean depth are governed by dynamic indices such as timing, duration, and amplitude of water level changes. A rise in reservoir/lake level leads to the submerging of terrestrial vegetation, which results in nutrients leaching from decomposing organic matter [14, 24]. Flooding of the marginal areas and increased river flow result in better conditions for spawning, growth, and survival of juveniles.

Furthermore, extreme water level fluctuation can change the diversity of invertebrates, especially those who are unable to migrate, and rapidly recolonize the drawdown zone [33]. Most of them die within a few hours when left stranded above the receding water. Eventually, species with a high tolerance to water level fluctuation such as chironomid and oligochaetes dominate. Also, Szluha et al. [20] observed that chironomids and oligochaetes larvae retreated deeper into the substrate and survived for 50–100 days following drawdown. They were also able to recolonize the littoral zone during the rising water levels. The consequences are less diversity of invertebrates with a high proportion of benthic invertebrate populations than those of undisturbed systems. Since invertebrates form, key links in reservoir food webs decrease their biodiversity and threaten the survival of other organisms in higher trophic levels including fish. Nutrient loading and recycling therefore significantly affect fish reproduction, primarily through their impacts on water quality, habitat quality, and food availability. Nutrient loading and recycling also can cause algal mats or dense plant growth which may increase sedimentation rates, leading to changes in substrate composition and habitat availability for fish. Loss of suitable spawning substrates or changes in water flow dynamics can hinder fish reproduction and recruitment.

2.2.2. Predator-Prey Relationship. Water level fluctuation also influences the predator-prey relationship. Findings by Leira and Cantonati [9] and Clarke et al. [40] demonstrated that rapid reservoir fluctuations influence predator-prey interactions. The average prey densities were lowest during the early summer when the water level was relatively high.

Also, in reservoirs, where water levels fluctuate dramatically, turbidity is often the most important abiotic factor influencing predator performance [32]. Highly turbid conditions reduce prey encounter rates. Predators' consumption rates are low under high turbidity conditions, while their energetic demands are high. They increase foraging effort and energy expenditure, as prey encounter rates decrease. Nevertheless, water level fluctuation reduces shelter availability for fish prey to hide; hence, they are more susceptible to predation. Fischer and Öhl [22] observed a distinct hierarchy in burbot (Lota lota) with respect to shelter occupation when such structures became scarce due to lowered water levels.

The predator-prey dynamics within aquatic ecosystems can have significant effects on fish reproduction success. The presence of predators can influence the behavior of spawning fish. Fear of predation may cause fish to avoid or delay spawning in areas where predators are abundant. On the other hand, fish may alter their spawning behavior, such as choosing different times or locations to spawn, in an attempt to minimize predation risk. These behavioral changes can affect the timing and success of spawning events, potentially reducing the reproductive output. Predators may target adult fish as prey, particularly during vulnerable life stages such as spawning. Predation pressure on adult fish can lead to reduced survivorship, limiting the number of individuals available to participate in spawning activities. High levels of predation on adult fish can also disrupt social structures within populations, impacting mating behaviors and reproductive success.

3. Effect of Water Level Fluctuation on Spawning, Larvae Development, and Survival of Juveniles

The literature on the effects of water level fluctuation on fish spawning activities exists. The phenomenon is believed to interfere with spawning and the development of larvae and juveniles [41]. Several authors reported that unfavorable water level fluctuation disrupts the spawning cues [7, 40, 43, 46]. Others say that it delays and decreases the hatching success of eggs due to air exposure of eggs [42, 44, 45]. Some authors argue that water level fluctuations reduce the survival of juvenile fishes [38–40]. Kahl et al. [41] reported that decreasing water level shortly after the spawning period was found to result in a total loss of the new roach year class.

Spawning is a metabolically demanding activity, in the life history of fishes, whether occurring as a single event or multiple-spawning seasons [35]. Fish allocate energy available to their physiology maintenance, somatic growth, storage, and reproduction [36]. Mature fish use their surplus energy to migrate to spawning grounds, courtship, complete a clutch of eggs, and parental care [35]. While some fish feed and spawn at the same places, others need to leave their feed ground to spawn. These fish species need to store energy for reproduction once conditions are favorable [36]. For these fish species, reproduction is constrained by physiological reserves and environmental cues that the eggs and larvae will experience. Both, physiological reserves and environmental cues are influenced by the water level fluctuation.

Fish species, which impose a closer spatial and temporal association between feeding to acquire energy and its use for spawning, constantly adjust reproductive efforts to food intake [35]. Therefore, environmental cues that inform them about food availability, such as flooding, are directly related to egg production and spawning. Conditions such as low flow, low floods, and hence low water level may lead to few egg production, delayed or skipped spawning to conserve energy for growth, and own physiology maintenance.

The basic requirements for successful spawning, development, and growth are therefore adequate spawning habitat, stable water level, and adequate food supply [20]. Water level fluctuation can significantly affect all of these requirements. When conditions are not favorable for spawning, females delay spawning by reabsorbing their eggs and males reabsorb their sperm [36]. Through their survival instincts, fish decide to put protein back into their own body, rather than to make futile attempts at dropping them in an environment that is too harsh for their offspring to survive.

Observations on the fish populations conducted for several years in numerous reservoirs revealed that water level fluctuation is the major factor affecting optimum fish production [20]. Water level fluctuation affects food

availability, fish energy accumulation [24], and the amount of energy invested for reproduction activities such as egg production and spawning. Furthermore, delayed or skipped spawning has been linked to poor feeding conditions and insufficient energy accumulation [36]. A life history model developed by Wantzen et al. [37] suggests that at very low energy, spawning is skipped. Starved females of white crappie failed to produce vitellogenic oocytes, whereas those who received high rations successfully developed vitellogenic oocytes [36].

Habitat is an important component of fish reproduction. It not only provides spawning grounds but also shelters for larvae and juvenile fish. A zooplanktivore fish, which was the most abundant fish in Lake Kinneret, was observed to spawn in winter when water levels rise and adhere its eggs to freshly inundated stones in shallow water [4]. The rise in water level in this case seems to have changed the environment such as a rise in water temperature that could have triggered the fish to spawn. Seasonal changes that cause water temperatures to rise dramatically in shallow water can influence fish spawning activities. Inundated plants also provided the fish larvae emerging from the eggs with sufficient shelter from predators, increasing their survival rates [2].

While macrophytes often provide a preferred spawning ground for many fish species, littoral zones provide spawning grounds for others [5]. Therefore, water level rise, which often favors the growth of macrophytes and inundation of stone substrates, stimulates spawning activities. The reproduction success of *Acanthobrama terraesanctae* was correlated with rates and magnitude of water level rise [16]. The years of exceptional water level rise were followed by population explosions of the species [5]. Their explanation for this correlation was that the availability of substrate for attaching the eggs was hugely increased relative to years of more typical WLF. Furthermore, newly inundated terrestrial plants were much more abundant in years of extreme water level rise than under the typical water level fluctuation regime in Kinneret, and terrestrial plants proliferate in the exposed shores during years of unusually low water levels and are inundated when the levels rise. These inundated plants provided the fish larvae emerging from the eggs with ample shelter from predators, increasing their survival rates.

Since most fishes spend a portion of their life cycle in the littoral zone, structures and conditions such as substrate type, food availability, and water chemistry influence the survival and reproduction success of fishes.

Essential reproduction processes such as spawning, incubation, and hatching of eggs and the development of larvae, postlarvae, and juveniles occur in the littoral zone. The early life stages of fish are particularly vulnerable with mortality rates of up to 99% recorded for a large number of species [31]. High mortality rates result from the limited swimming ability of larvae preventing them from escaping suboptimal environmental conditions, predators, or low prey density areas [31]. Availability of spawning habitats, and food resources, thus determines the spawning success and development of young fishes. Water level fluctuation therefore strongly influences the reproduction success of fish due to its effects on the littoral zone.

4. Discussion

Figure 2 demonstrates the cascading effect of water level fluctuations on fish reproduction success as outlined in the literature reviewed. Water level fluctuations stand both increases and decreases in the water level of the reservoir/lake, which may be due to high downstream outflow or reduced inflow. The extent and direction of these effects depend on the frequency, magnitude, and duration of the fluctuations, as well as the specific species of fish and their life history traits [9, 50].

Water level fluctuation brings both opportunities and changes to fish lives. Increases in water levels associated with increased river inflow, especially during the rainy season have been reported to bring in organic matter, thus increasing food availability to lentic water bodies [51]. Fluctuations can change the distribution of food resources for fish, for example, a sudden drop in water levels may concentrate prey species in smaller areas, making it easier for fish to find food [52]. Conversely, rising water levels can disperse prey, potentially making it more challenging for fish to forage effectively.

Water level fluctuations that expose or submerge nesting sites can immediately lead to reduced reproductive success. It may dislodge fish eggs from their nesting sites or expose them to desiccation or predation. This can lead to higher mortality rates for eggs and newly hatched fry (Figure 2). Water level fluctuations may introduce new predators into fish habitats, which can lead to increased predation pressure on certain fish species, particularly during vulnerable life stages such as fry and larvae.

Rapid or extreme water level fluctuations can disrupt fish spawning and egg incubation [35, 36]. Many fish species rely on specific water depths and substrate types for successful reproduction. Water level fluctuations can alter the flow regime, affecting the transport of fish eggs and larvae downstream [50]. In some cases, this can result in reduced survival and recruitment of juvenile fish.

The most significant abiotic elements impacting aquatic species' breeding efficiency are temperature and dissolved oxygen [53]. Optimally balanced combinations of temperature and dissolved oxygen have been associated with the largest quantity and quality of fingerlings produced [53]. Rapid drops in water levels have been associated with decreased oxygen availability in the water of the water column, which can stress fish and impact their metabolic functions, and general fish physiology and hence affect their reproduction success [42, 44, 45, 53]. This is particularly problematic for fish that require well-oxygenated waters, such as salmonids. Fluctuations in water levels can also influence water temperature. Sudden changes in temperature can be stressful for fish, affecting their metabolism, growth, and behavior. Fish may experience altered hormone levels due to temperature fluctuation stress leading to withdrawl or delayed spawning [53–55]. This can affect their overall health and reproduction.

Fish that need to migrate or move within a water system may find it challenging to navigate obstacles such as sudden drops or increases in water levels. This can hinder their

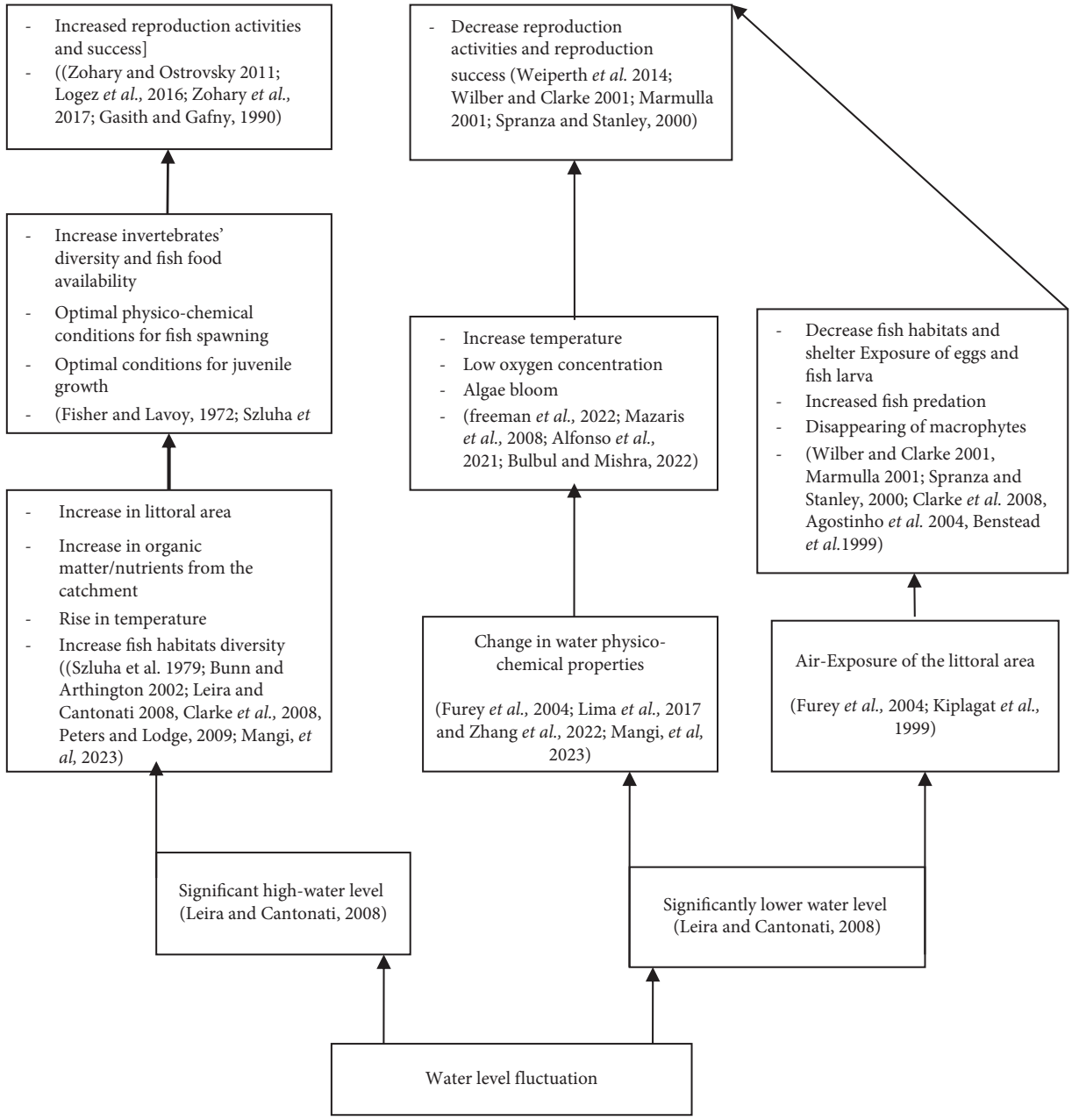

Figure 2: Cascading effect of water level fluctuation on reservoir/lake fish reproduction success.

ability to access important habitats for food and reproduction activities [35]. Nevertheless, some species have adapted to tolerate and even benefit from these changes, while others are more sensitive.

5. Conclusion

The literature reviewed shows that water level fluctuation is a natural phenomenon with both positive and negative effects on lakes and reservoirs' fish physiology and reproduction success. The dual nature of the phenomenon complicates the topic. The effects of water level fluctuation on fish reproduction are complex and depend on various ecological factors. While some fluctuations may create favorable conditions for reproduction, others can pose challenges and threaten the sustainability of fish populations.

Nevertheless, most of the literature reviewed supports that the severity of the effect is dependent on the magnitude, duration, time of the fluctuation, and the species exposed. The quantification of moderate and extreme water level fluctuations and associated effects is lacking. Most of the articles reviewed support moderate fluctuations, arguing that they have more positive than negative impacts, whereas extreme fluctuations tend to bring more adverse impacts on fish reproduction processes. Few articles indicate the range of decrease or increase of water level, duration of such events, and effects they have on reservoir/lake ecosystem

functions, fish physiology, and/or reproduction. It is concluded that water level fluctuation is an important environmental process for fish reproduction success, however, moderation of extreme water level variations, especially multiannual variation is vital for fish reproduction [56].

5.1. Recommendation. Enhancing fish reproduction success in the environment of fluctuating water levels requires a balanced approach that considers the needs of both fish and the broader aquatic ecosystem structures and functions. To achieve this goal, the following must be taken into consideration:

(i) Managers should understand the patterns and trends of water level fluctuations for developing effective management strategies.

(ii) Upstream water use and reservoir operations should take into consideration the effects of water level fluctuations on lakes or reservoir structure and the biological functions of fishes in order to maintain their optimal growth and reproduction success.

(iii) Water management activities such as dam operations or water releases should be well coordinated to minimize disruptions during critical periods for fish reproduction such as spawning seasons. It is important to adjust water release schedules to mimic natural flow patterns as much as possible.

(iv) Adaptive management practices that allow for flexibility and adjustment based on monitoring data and feedback from stakeholders should be implemented.

(v) Since different fish species are affected differently by water level fluctuations, due to varying requirements for spawning and reproduction, further research should be undertaken to understand the specific habitat preferences and reproductive behaviors of target fish species in a specific area.

(vi) Continuous evaluation of the effectiveness of management strategies and adjustments to improve outcomes for fish reproduction should be regularly conducted.

Data Availability

The data used to support the findings of this study are available within the article.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

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